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ECOGRAPHY

Review and synthesis

Shellfish subsidies along the Pacific coast of North America

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Spatial subsidies are associated with pronounced ecosystem responses, as nutrients cross ecological boundaries and cascade through food webs. While the importance of subsidies is known, the role of shellfish, specifically molluscs, as a marine subsidy has not been formally described. Focusing primarily on the Pacific coast of North America, we identify vectors that transport shellfish-derived nutrients into coastal terrestrial environments, including birds, mammals, and over 13 000 yr of marine resource use by people. Evidence from recipient ecosystems suggests shellfish drastically influence soil chemistry, forest productivity and the diversity of primary producers at the regional and landscape level. Responses in higher trophic levels have not yet been investigated, but given documented responses in lower trophic levels, this may be due to a lack of examination. To determine if the processes we describe within the northeast Pacific are pertinent to coastal environments worldwide, we also explore shellfish subsidies globally, with a specific focus on temperate and tropical islands. As shellfish are not as spatially or temporally constrained as other subsidies, our examination suggests our findings are applicable to many other geographical regions along the marine–terrestrial interface.

Keywords: coastal ecology, food webs, marine molluscs, marine-derived nutrients, spatial subsidies

Marine subsidies

Marine subsidies occur when nutrients are transferred from marine to terrestrial ecosystems, anywhere along the 594 000 km of global coastline (Hammond 1990). These subsidies can take the form of seabird guano (Sánchez-Piñero and Polis 2000), marine mammal carcasses (Polis and Hurd 1996), spawning fishes (Fox et al. 2015, Reimchen 2018) or macroalgae deposition (Spiller et al. 2010). While all of these subsidies play important roles in shaping terrestrial productivity, their effect sizes vary over space and time. For example, relatively brief, intense pulses of marine nutrients are deposited in riparian forests during annual Pacific salmon *Oncorhynchus* spp. autumn spawning (Gende et al. 2002, Reimchen et al. 2003, Reimchen 2018),



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while beaches generally receive marine nutrients year-round through macroalgal deposition (Barreiro et al. 2011). Spatial variation in marine subsidy strength also mediates the extent that terrestrial ecosystems respond (Darimont et al. 2009). At some point, all marine subsidies decrease in availability with increasing distance from the source (e.g. increasing distance inland, Polis and Hurd 1996), but their effect is context specific. For example, the effects of macroalga-derived nutrients on abundances and diets of terrestrial consumers (e.g. spiders and mice) decline within 200 m from shore (Polis and Hurd 1996), while salmon-derived nutrients within grizzly bear *Ursus arctos* diets extends for hundreds of kilometers inland (Adams et al. 2017). These marine-derived nutrients are often limited in the temperate forests along the Pacific coast of North America and critical to recipient ecosystems (Box 1).

The effects of marine subsidies are seen at multiple trophic levels, from the fertilization of plants, to the numerical increase of prey (e.g. terrestrial arthropods) for terrestrial consumers (Spiller et al. 2010, Collins and Baxter 2014). Additionally, marine subsidies can have more nuanced and complex implications for the recipient communities. Hocking et al. (2013) found that Pacific salmon subsidies can increase the body size-biomass relationships in terrestrial fly larvae (*Cyclorrhaphan*), creating a temporary 'escape' from body size restrictions during autumn salmon spawning. Rich marine resources can also facilitate intra-population niche variation in large terrestrial carnivores, and influence trophic interaction strength (Darimont et al. 2009, Adams et al. 2017).

The wide-reaching effects of marine subsidies, particularly Pacific salmon and marine bird guano, have been thoroughly documented compared to other less visible and therefore less considered avenues of marine subsidy. Spatial subsidies not associated with large pulses of nutrients and energy transfer

are rarely considered despite their potential to be more temporally and spatially available than conventionally considered subsidies. Despite global distribution and easy accessibility, the role of shellfish as a marine subsidy has never been formally considered or evaluated in modern science. Fortunately, a growing literature on the prevalence and importance of shellfish-derived nutrients transferred into adjacent terrestrial ecosystems has laid the foundation for evaluating the role of shellfish as a spatial subsidy (Erlandson and Moss 2001, Carlton and Hodder 2003, Cook-Patton et al. 2014, Trant et al. 2016, Fig. 1a–c). As a subsidy, shellfish occupy the entire Pacific Coast of North America, in relatively stable abundances that exhibit limited seasonal fluctuations. Therefore, despite being relatively less concentrated than pulse-driven subsidies such as salmon, shellfish have a higher spatial and temporal availability, with comparatively more stable intra-annual abundances (Gosling 2008), which allows shellfish-derived nutrients to contribute to a significant portion of coastal ecosystems for a more extended period.

Here we present an overview of shellfish as a marine subsidy to coastal terrestrial ecosystems along the Pacific coast of North America. We primarily focus on molluscs, specifically bivalves including clams, oysters and mussels, but acknowledge other shellfish as well (e.g. abalone, crabs). We consider the vectors (birds, mammals and humans) that transport shellfish into coastal terrestrial ecosystems, the abundance of shellfish-derived nutrients transported, and the prolonged persistence of shellfish subsidies once deposited within terrestrial ecosystems. We also summarize known and potential implications for recipient ecosystems. Our evaluation focuses primarily on coastal regions and processes occurring along the Pacific coast of North America due to the area's known importance as an intact model ecosystem highly influenced by various marine subsidies (Reimchen et al. 2003,

Box 1

Marine-derived nutrients are commonly rich in nitrogen (N), phosphorus (P) and lipids, which are limited in temperate terrestrial ecosystems (Vitousek and Howarth 1991, Elser et al. 2007). This limitation is primarily due to a lack of symbiotic N fixers (Vitousek and Howarth 1991), insufficient lipid sources, and young soils, which impact the potential for P sequestration via mineralogical transformations (Walker and Syers 1976). Nitrogen is an essential element present in amino acids, which form the building blocks of proteins, promote growth and facilitate development (Elser et al. 2007). Phosphorus is a component of nucleic acids, which promotes protein synthesis, cell division and the development of new tissues (Walker and Syers 1976, Newman 1995). Within plants, for example, N and P availability influences key processes like photosynthesis, seed formation and biomass accumulation (Walker and Syers 1976, Sinclair and Horie 1989, Newman 1995). Marine-derived lipids are essential fatty acids such as eicosapentaenoic acid (EPA) and docosahexaenoic acid (DPA), which support numerous species' physiological processes related to the central nervous system, the cardiovascular system and the immune system (Twining et al. 2016).

These critical nutrients help support relatively high productivity within terrestrial environments that otherwise might exhibit much lower productivity. Consequently, throughout the Pacific coast of North America, the flow of marine-derived nutrients into terrestrial ecosystems supports healthy, thriving, ecosystems (Gende et al. 2002). The enrichment of terrestrial ecosystems with marine-derived N and P among other nutrients produces positive synergistic responses (Elser et al. 2007). These nutrient subsidies can be measured using stable isotope analysis. As terrestrial N and carbon (C) sources undergo less trophic accumulation, isotope ratio mass spectrometry allows for enriched marine N and C to be detected within terrestrial ecosystems. Elevated enriched N and C signatures in terrestrial consumers indicates a marine-based diet (Darimont et al. 2009), while enriched N but not C is indicative of the indirect consumption of marine nutrients (Hocking and Reimchen 2002). Furthermore, the coupling between marine-derived nutrients and primary productivity allows for marine nutrients, especially N, to be detected within the annual growth rings of trees. This allows old growth forests to serve as an archive of marine subsidy abundance (Reimchen et al. 2003, Reimchen 2018, Reimchen and Arbellay 2018).

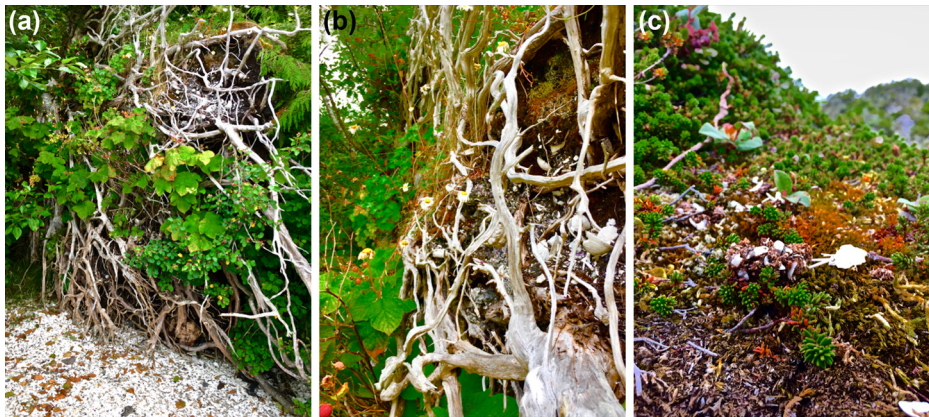


Figure 1. (a) Shell fragments litter the high intertidal of beaches along British Columbia's central coast. (b) Shellfish remains can be seen woven within the root structures of fallen trees, commonly associated with a diversity of flora. (c) Mollusc remains, possibly *Mytilus trossulus*, deposited as scat, atop Calvert Island, West beach lookout, at an elevation of over 60 m a.s.l.

Fox et al. 2015, Reimchen 2018). The global distribution of shellfish suggests these findings are pertinent to many other geographical areas with a marine–terrestrial interface. To evaluate the broader relevance of our findings, we consider shellfish subsidies globally, with a focus on islands as specific regions of interest, and the worldwide human consumption of shellfish. This evaluation illustrates that the processes we describe in the northeast Pacific likely apply to marine–terrestrial interfaces worldwide.

Vectors of shellfish transfer into terrestrial systems

Coastal birds

Numerous species of coastal bird's forage in the intertidal zone, and carry shellfish back to their nests to consume or feed to their offspring (Fig. 2a–c). Well-known for their consumption of salmon and scavenged mammals, bald eagles *Haliaeetus leucocephalus* along the Pacific coast of North America also consume a substantial amount of abalone, mussels and other molluscs (Grubb and Hensel 1978, Erlandson and Moss 2001). In a similar fashion, multiple gull and crow species, including common gulls *Larus canus*, kelp gulls *Larus dominicanus* and northwestern crows *Corvus caurinus* consume an assortment of marine organisms including mussels and clams (Siegfried 1977, Erlandson and Moss 2001). Gulls and crows also engage in shell dropping behaviour to crack open shellfish and gain access to the flesh, which occurs on hard substrates, occasionally up to 240 m away from the collection location (Siegfried 1977, Whiteley et al. 1990, Erlandson and Moss 2001). Additionally, surf *Melanitta perspicillata* and white-winged *Melanitta fusca* scoter ducks prey predominantly on clams and other molluscs; bivalves account for over 70% of the total fecal dry mass (Lewis et al. 2007). These species prey on Manila clams *Venerupis philippinarum* and varnish clams *Nuttallia obscurata*, with a case study indicating that over three million clams were removed

from sites within the Strait of Georgia, British Columbia by scoter ducks in a single season (Lewis et al. 2007).

Birds as vectors for shellfish subsidies deposit substantial amounts of shellfish remains in terrestrial ecosystems. These remains form middens under nests, often at the base of trees, that have been mistaken for long-term archeological deposits due to their size and age (Erlandson and Moss 2001). The presence of avian-derived shellfish middens hundreds of meters inland have been observed adjacent to gull, eagle and crow nesting sites and colonies (Erlandson and Moss 2001). Along the Oregon coast, seagull middens of 100 m² contain thousands of fragments of mussel *Mytilus californianus*, crabs *Cancer* spp., chitons (Polyplacophora) and other shells (Erlandson and Moss 2001). Furthermore, these birds, which may be nesting at coastal margins to take advantage of the shellfish food source, excrete substantial amounts of nitrogen and phosphorus, derived in part from their consumption of shellfish. As such, coastal birds create large middens of accumulated shellfish-derived nutrients, and as a consequence, deposit nitrogen- and phosphorus-rich guano across vast portions of coastal terrestrial ecosystems (Fig. 2a–c, Fig. 3). These nutrients subsequently accumulate within terrestrial ecosystems and positively affect primary and secondary productivity (Cocks et al. 1998).

Coastal mammals

Coastal mammals often rely heavily upon marine-derived food, especially shellfish (Fig. 2d–h). Through inter- and sub-tidal foraging, coastal mammals act as vectors for marine nutrients in a similar manner as avian vectors, scattering shellfish remains throughout the terrestrial environment during feeding activities and excretion (Erlandson and Moss 2001, Carlton and Hodder 2003). While the opportunity to forage intertidal shellfish or scavenge shellfish remains is utilized by almost every mammalian trophic level, from insectivorous shrews to apex carnivores such as bears, many species rely upon shellfish as a major constituent in their diets (Carlton and Hodder 2003).



Figure 2. Vectors that transport shellfish-derived nutrients into northwest Pacific terrestrial ecosystems. (a–c) Bald eagles *Haliaeetus leucocephalus*, gulls *Larus* spp. and crows *Corvus caurinus* consume shellfish, create middens below nests and engage in shell-dropping. (d–f) River otters *Lontra canadensis*, mink *Neovison vison* and raccoons *Procyon lotor* forage subtidally, returning to terrestrial areas to consume and excrete prey. (g) Sea otters *Enhydra lutris* frequent haul-out sites and contribute feces. (h) Grizzly bears *Urus arctos* transport shellfish fragments several kilometers inland. (i) Clam gardens, clam digging and associated large shellfish middens from coastal First Nations have contributed to substantial transfer of shellfish-derived nutrients. (j) Over 13 000 yr of coastal habitation has involved extensive cultivation, harvesting and consumption of shellfish by coastal people. In many instances, these shellfish-derived nutrients are transported great distances inland.

Several mustelid mesopredators are responsible for transporting and depositing shellfish along coastlines. River otter *Lontra canadensis* forage subtidally for fish and shellfish, but return habitually to terrestrial platforms up to 20 m inland to consume and deposit prey (Larsen 1983, Ben-David et al. 1998). At these locations, middens of considerable size accumulate the hard remains and unconsumed flesh of prey such as abalone and mussel shells, urchin tests, crab carapaces and chiton skeletons (Haggarty et al. 1991, Bowyer et al. 1994). In extreme cases, middens of 96 m² containing hundreds of shellfish fragments have been documented (Erlandson and Moss 2001).

Likewise, river otter latrine sites are laden with marine-derived nutrients and fragments of shellfish prey (Stenson et al. 1984, Erlandson and Moss 2001). While most studies focused on the Pacific highlight the importance of fin-fish (as opposed to shellfish) in river otter diets (Stenson et al. 1984, Ben-David et al. 1998), bivalves, gastropods, crustaceans, chitons and other shellfish, can account for over half of their food consumption (Bowyer et al. 1994). However, Bowyer et al. (1994) observed consumption of only soft viscera of mussels *Mytilus edulis* and scallops *Chlamys* spp., material that would not be detected when analyzing faecal samples

or gut contents. The combination of shell-laden midden sites and this observation suggests shellfish are an important, but possibly underestimated prey source.

Similar to river otter, mink *Neovison vison* also create middens and latrine sites littered with shell fragments. Along the Pacific coast from Washington to Alaska, mink have been recorded consuming bivalves, gastropods, crustaceans and echinoderms (Hatler 1976, see records in Carlton and Hodder 2003). Hatler (1976) reported predation on shellfish to be rare, but noted that mink will scavenge soft parts of shellfish (e.g. horse clam siphons), or dissect out soft internal viscera from clams (Svihla and Svihla 1931). In addition, mink will cache or hide food underground for later consumption, which may supply another route of subsidies to the terrestrial environment (Hatler 1976, Erlandson and Moss 2001). Furthermore, we have observed many mink latrine sites littered with abalone shells, urchin tests and chiton exoskeletons, which suggests mink (and possibly other consumers) may eat only the soft components of shellfish prey (Davidson unpubl.).

Raccoons *Procyon lotor*, are also opportunistic mesopredators that will capitalize on intertidal prey. While most of this predation is focused on crabs and fish, consumption

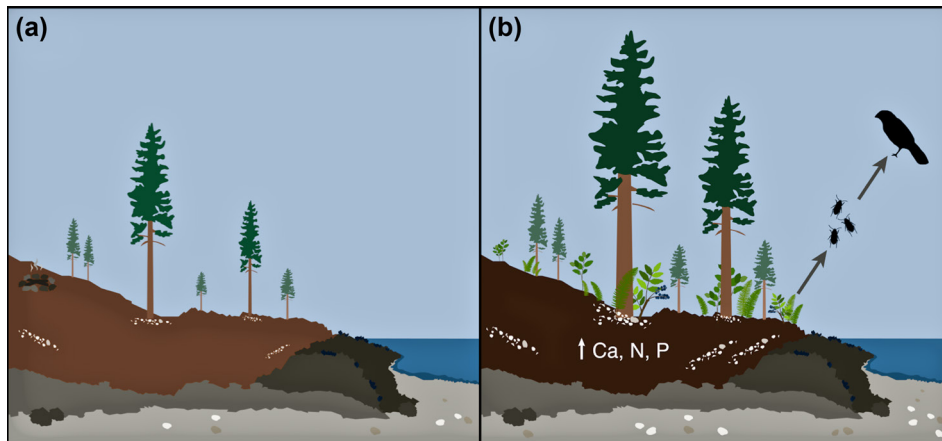


Figure 3. (a) Coastal ecosystem with shellfish nutrient influx from animals and human habitation (including terracing). (b) Coastal ecosystem response to added shellfish nutrients including an increase in soil nutrients (especially calcium, nitrogen and phosphorus), greater radial growth and increased height of trees, and a greater abundance and diversity of vegetation that may support a more diverse community of insects and potentially birds.

of bivalves and gastropods occurs from Oregon to British Columbia (see records in Carlton and Hodder 2003), as evident by remains of mussels in terrestrial latrine sites (Simmons et al. 2014). Raccoons can consume 7.5 ± 3.2 clams per 5 min, often choosing species that maximize energy intake (Simmons et al. 2014). The result being a substantial amount of shellfish-derived nutrients, including nitrogen and phosphorus, entering terrestrial ecosystems via excretion and urination by raccoons. As opportunistic mesopredators, raccoons may contribute a more dynamic range of shellfish-derived nutrients into terrestrial ecosystems than many other coastal mammals.

Perhaps less documented, and rarely considered a key marine subsidy vector, is the terrestrial activity of sea otters *Enhydra lutris*. While they are often described as the keystone predator that specializes in red sea urchins *Mesocentrotus franciscanus*, observational studies indicate that they will switch to clams, other bivalves and crustaceans once urchin populations are depleted, especially when large sea otter colonies occupy soft-sediment habitats (Kvitek et al. 1988, Rechsteiner et al. 2019). In certain instances, the clam species *Tresus nuttallii* and *Saxidomus nuttalli* can comprise over half of the prey harvested from nearshore habitats (Kvitek et al. 1988). Sea otters will frequently haul-out to rest on rocky points, sand beaches and even grassy areas (up to 75 m inland) adjacent to their offshore feeding grounds, where large quantities of fecal matter are deposited (Kenyon 1969). In the Aleutian Islands, haul-out sites are used habitually and frequently, with accumulated fecal deposits containing up to 94% mollusc and crustacean remains (Kenyon 1969).

Bears, due to their relatively high density along the coast, substantial metabolic requirements, and large home ranges, may be one of the more predominant vectors of shellfish nutrients into terrestrial ecosystems via scat and urination. Grizzly bears (*Ursus arctos*) spend up to 5% of their time digging for clams, where they can catch and consume 1–2 clams

a minute (Smith and Partridge 2004). As bears are highly mobile there is elevated potential for the marine shell fragments to be transported several kilometers inland from the coast (Erlandson and Moss 2001). Haggarty et al. (1991) observed such transport along the Alaskan Peninsula, where low-density surface scat has accumulated from thousands of years of bear activity, and can be seen adjacent to fresh meter-wide clusters of scat containing high concentrations of bivalve shell fragments.

It is important to note that most dietary studies focus upon morphological examination of fecal content. These studies may underestimate the importance of shellfish, as many consumers are able to remove and consume only soft parts of shellfish which are not detectable using most conventional visual scat analysis methods. For example, mink and raccoon are more dexterous than many other shellfish consumers, and can crush and pry open clams to consume the soft viscera (Svihla and Svihla 1931, Simmons et al. 2014). Similarly, sea and river otters may break open shells or tests using force (or tools in the case of sea otters), allowing for the consumption of only soft viscera. These abilities, combined with the common occurrence of shells and exoskeletons in mammal latrines and middens (Davidson unpubl.) suggest that shellfish are an important, but possibly under-appreciated marine subsidy. Furthermore, urination by coastal mammals contributes a substantial amount of marine-derived nutrients into terrestrial ecosystems, especially nitrogen, but is less evident than scat or shell remnants. For example, up to 97% of the nitrogen deposited by brown bears onto the riparian area is added via urination (Hilderbrand et al. 1999). It is reasonable to assume this process is similar whether the nitrogen is derived from fish or shellfish, and supports the notion that current inputs of shellfish-derived nutrients are vast underestimates. Furthermore, given the number of coastal mammals that forage in nearshore habitats (Carlton and Hodder 2003), it is likely that numerous other mammals not discussed here

also consume shellfish and act as vectors for nutrient transfer inland via direct deposition, excretion or urination (e.g. *Canis lupus*).

Coastal humans

Marine-derived foods have been critical for sustaining coastal human populations since time immemorial. Coastal First Peoples have migrated along the Pacific coast of North America for over 13 000 yr, inhabiting coastal refugia during glaciation, and sustaining populations by accessing marine foods via watercraft and cultivation (Lepofsky et al. 2015, McLaren et al. 2018). Among other seafoods, marine shellfish were, and continue to be, key food sources for coastal communities (Deur et al. 2015, Lepofsky et al. 2015, Jackley et al. 2016), with the occupation of Coast Salish winter villages and shellfish-harvesting camps, including those within the Strait of Juan de Fuca, Washington, being largely driven by the availability of marine resources (Hutchinson et al. 2019).

To ensure a consistent, easily-accessible supply of shellfish, some coastal communities engineered extensive clam gardens near habitation sites (Fig. 2i, Lepofsky et al. 2015, Jackley et al. 2016). Constructed by building rock walls in the mid to low intertidal, clam gardens increase sedimentation rates by at least four-fold, which alters the beach slope at tidal heights optimal for clam production (Groesbeck et al. 2014, Deur et al. 2015, Neudorf et al. 2017). These intertidal rock walls and associated terraces represent one of several coastal habitat alterations created over millennia by Coast Salish people to steward marine resources, increase clam productivity and ensure stable shellfish abundances adjacent to coastal communities to support economies, cultural practices and governance (Lepofsky et al. 2015, Hul'q'umi'num – GINPR 2016). Recent radiocarbon dates and scientific investigations into taphonomic processes, indicate clam garden construction throughout Northern Quadra Island, British Columbia, began at least 3500 yr before present (Smith et al. 2019). In addition to supplying a reliable food source for communities, clam gardening is integral to governance systems that dictated land use and stewardship, which continues to the present day (Deur et al. 2015, Lepofsky et al. 2015, Hul'q'umi'num – GINPR 2016). The thousands of clam gardens heterogeneously distributed along the coast provide not only an opportunity to appreciate the complexities of traditional resource management (Harper 2007, Deur et al. 2015, Lepofsky et al. 2015, Hul'q'umi'num – GINPR 2016), but also an indication that shellfish play an important role in sustaining coastal populations (Harper 2007, Deur et al. 2015, Lepofsky et al. 2015), and that certain communities transfer shellfish-derived nutrients into terrestrial ecosystems at substantial rates.

Once harvested and consumed, large quantities of shell and fragments were scattered throughout coastal forests for various functions. Shellfish remains were terraced into soil to modify sloping landscapes into flat, leveled areas, potentially forming the foundation for housing structures or other buildings (Sawbridge and Bell 1972, Blukas-Onat 1985). Concurrently, shell middens improved habitat and soil

drainage for culturally important terrestrial plants (Trant et al. 2016, Fisher et al. 2019). Alternatively, shellfish remains were deposited as refuse into middens adjacent to settlement areas. Long-term consumption of shellfish has resulted in middens that have been active for well over 5000 yr of continuous use (Cannon and Yang 2006), with vocation largely driven by consistent availability of marine resources, including shellfish (Cannon and Yang 2006, Hutchinson et al. 2019).

These shellfish deposits, which are common along the Pacific coast of North America, can reach over 5 m in depth, span hundreds of square-meters, and extend up to 110 m inland (Erlandson and Moss 2001, Cannon and Yang 2006, Cook-Patton et al. 2014). The number of shellfish deposits along the Pacific coast of North America remains largely unresolved, however, substantial efforts by First Nations heritage managers and by archaeologists has elucidated at minimum 5300 recorded coastal shell deposits that exist along the coast of British Columbia (McKechnie 2013). The Broken Group archipelago, for example, contains at least 73 shell deposits (McKechnie 2013). The result of long-term human occupation throughout the region, many of the deposits are associated with houses, terraces, and connected to Indigenous oral history of the villages. Collectively, the deposits amass more than 114 000 m² of shellfish remains spread throughout the archipelago (McKechnie 2013). If representative, this observation suggests that tens of thousands of shell deposits, amassing millions of cubic meters of shellfish-derived nutrients, may exist along the Pacific coast of North America.

Although the amount of shellfish transported by humans into terrestrial ecosystems remains unquantifiable, cultural practices such as clam gardening, and the longstanding practices surrounding shellfish resource management, suggest that shellfish-derived nutrients have been, and will continue to be, deposited in large quantities into terrestrial ecosystems by coastal human populations.

Shellfish out of water

Shellfish-derived nutrients

Shellfish are commonly deposited as hard shells and shell fragments in the terrestrial environment, impacting both physical and chemical properties of terrestrial forests. Additional nutrients are also supplied to forests through excretion and discarded soft viscera. Used for terracing by coastal First Nations, or discarded as refuse by coastal people, mammals or birds, hard shells and shell fragments act as a coarse, bulk material, improving soil drainage while maintaining stability (Ceci 1984, Trant et al. 2016). Moderately drained, nutrient-rich soils promote growing conditions for primary producers (Sawbridge and Bell 1972, Knicker 2011, Trant et al. 2016). Shellfish middens commonly co-occur with other components of coastal First Nations' long-term management of terrestrial ecosystems, including charcoal from fires or controlled burns (Hoffman et al 2016, 2017, Trant et al. 2016). With mixed-severity controlled burns recurring at minimum

for six centuries as part of coastal First Nations stewardship (Hoffman et al. 2016, 2017), shellfish nutrients deposited by coastal birds and mammals, would be exposed to similar conditions. The addition of calcium carbonate and charcoal causes the surrounding soil pH to increase, which facilitates the availability of phosphorus and other macronutrients, increases the soils cation exchange capacity and biotic activity, and promotes porosity (Johnson 1992, Demeyer et al. 2001).

The composition and quantity of shellfish-derived nutrients deposited in the terrestrial environment will vary based on the species considered, and the form it takes in the terrestrial environment (i.e. components of scat vs. hard body parts in middens). Generally, molluscs are low in fat (Nettleton and Exler 1992) and high in calcium carbonate and protein (Box 1; Gosling 2008). For example, a medium-sized (20 g) clam contains: 2.56 g of protein, 0.19 g of fat, 220 mg of nitrogen and 34 mg of phosphorus, while their shells are more than 90% calcium carbonate (Reitsma et al. 2017, Table 1). However, other shellfish contain more protein and essential fatty acids (Table 1). For example, 225 g of Pacific oysters, 175 g of blue mussels or 122 g of Dungeness crab would transfer comparable amounts of protein into the terrestrial environment as 100 g of sockeye salmon (Table 1). Furthermore, shellfish generally contain proportionally more unsaturated than saturated fats, which promotes development, growth and cellular functions in animals (Simopoulos 1991). For example, fatty acid composition in Dungeness crabs is 57% polyunsaturated fats, 23% mono-saturated and 20% saturated, with the Manila clam and Pacific oyster having similar ratios. Comparatively, salmon are composed of 37% polyunsaturated, 40% mono-saturated and 23% saturated (King et al. 1990). Shellfish-derived nutrients also represent considerable sources of minerals, including iron, zinc and copper, which are found in high quantities within shellfish compared to finfish (Table 1).

Whole shellfish (soft body plus shell) transported into terrestrial ecosystems are a rare occurrence; nutrients will either be transferred indirectly through feces or urination, or directly through shell and flesh deposits into middens and other high nutrient transfer areas (Fig. 3a). Driven primarily by shellfish deposits and centuries of forest stewardship, soil nutrients surrounding long-term habitation sites on the central coast exhibit higher levels of boron, calcium, manganese,

sodium, potassium, inorganic carbon, zinc, exchangeable calcium, and increased effective cation exchange capacity (Fisher et al. 2019). On the east coast of North America, middens comprised primarily of eastern oyster *Crassostrea virginica*, razor clam *Tagelus plebeius* and hard clam *Mercenaria mercenaria* shells in the Chesapeake Bay area exhibit soils with 45-times more calcium, 6.7-times more nitrates, a more neutral pH, and increased concentrations of other elements such as boron and manganese, relative to soils adjacent to middens (Cook-Patton et al. 2014). Compared to commonly considered spatial subsidies such as salmon that deposit primarily nitrogen and lipids, which become depleted relatively quickly (Johnson 1992), these nutrients can be more persistent (Cook-Patton et al. 2014) and have potential long-term cascading effects on terrestrial food webs.

Shell fragments and shellfish-derived nutrients persist in the terrestrial environment much longer than other marine-derived nutrients (e.g. $\delta^{15}\text{N}$ from salmon carcasses; Johnson 1992, Cook-Patton et al. 2014, Trant et al. 2016). Globally, excavation of middens deposited 70 000 yr before the present suggests that shellfish-derived nutrients, especially calcium, deposited into terrestrial ecosystems may persist until utilized (Volman 1978, O'Connor et al. 2002). Evidence from the northeast Pacific suggests that once transported inland shellfish-derived nutrients will decrease with time but have the potential to persist for millennia, and may influence forest ecosystems on boundless timescales (Sawbridge and Bell 1972, Trant et al. 2016, Fisher et al. 2019). These nutrients accumulate within coastal ecosystems by forming large mounds in the high intertidal, being incorporated into the root systems of the surrounding flora, or being deposited on hill tops by various vectors (Fig. 1a–c). Especially, calcium that is released slowly from degrading shells and is commonly deficient in forested ecosystems. Again, these processes persist well beyond the majority of the nutrients delivered during spatial and temporal limited subsidies, such as spawning Pacific salmon or herring.

Primary productivity responses

Shellfish remains contribute high levels of several nutrients, including calcium and phosphorus, to the soil surrounding deposit sites (Cook-Patton et al. 2014, Trant et al. 2016,

Table 1. Nutritional value of common shellfish and sockeye salmon, per 100 g of raw edible portion, including protein, fat, eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), iron, phosphorus, zinc and copper. Sources: King et al. (1990), Nettleton and Exler (1992), Martin et al. (2000), Dong (2001), Exler and Pehrsson (2007), Wright et al. (2018).

	Protein (g)	Total fat (g)	EPA and DHA (g)	Vitamin B12 (ug)	Iron (mg)	Phosphorus (mg)	Zinc (mg)	Copper (mg)
Pacific oyster <i>Magallana gigas</i>	9.45	2.3	0.69	16	5.11	162	16.62	1.58
Clam, mixed species	12.77	0.96	0.14	49	14	169	1.37	0.34
Blue mussel <i>Mytilus edulis</i>	11.9	2.24	0.44	12	3.95	197	1.6	0.09
Scallop, mixed species	16.78	0.76	0.103	1.41	0.38	334	0.9	0.05
Dungeness crab <i>Metacarcinus magister</i>	17.41	0.97	0.31	9	0.37	182	4.27	0.67
Sockeye salmon <i>Oncorhynchus nerka</i>	21.3	8.56	1.17	5	0.47	266	0.54	0.05

Fisher et al. 2019), while excretion and discarded soft viscera contribute substantial amounts of nitrogen, phosphorus, lipids and trace minerals to the riparian zone (King et al. 1990, Dong 2001, Reitsma et al. 2017). Furthermore, shell fragments facilitate favorable physical conditions within forest landscapes, which if co-occurring with additional features of long-term habitation (e.g. charcoal, terraced landscapes), are extremely advantageous for primary production (Hoffman et al 2016, 2017, Trant et al. 2016).

The slow release of calcium from degrading shells is a persistent source of nutrients for primary producers, while excretion and discarded soft viscera contribute nitrogen that is more readily available (Kennedy et al. 1969, Sawbridge and Bell 1972). If the surrounding conditions have facilitated decreased soil acidity (i.e. the presence of charcoal), decomposition of organic matter increases due to favorable conditions for microbial activity (Kuzyakov et al. 2000, Bardgett 2005). This increased carbon elicits fine root production in mycorrhizal fungi and supports root exudation (Treseder 2004). As mycorrhizal fungi stimulate nitrogen cycling by increasing the decomposition of organic matter in soils, capturing organic and inorganic nitrogen, and transferring nitrogen to host plants, soil conditions surrounding shellfish deposits increase primary producers' access to soil nitrogen (Kuzyakov et al. 2000, Hodge et al. 2001, Treseder 2004). As nitrogen often limits temperate forest productivity, increased uptake of nitrogen supports photosynthesis, plant reproduction and increases overall plant growth (Sinclair and Horie 1989, Newman 1995, Elser et al. 2007). As such, landscapes surrounding shellfish deposits, especially those subjected to centuries of forest stewardship, will have reduced carbon to nitrogen ratios, due to increased nitrogen, which allows plant species that would be otherwise nitrogen-limited to succeed (Sawbridge and Bell 1972, Fisher et al. 2019).

Increased nutrients, drainage and pH elicit increased productivity within plant communities above shellfish deposits. Trees growing adjacent to deposits exhibit greater radial growth and increased height, which decreases with increasing distance from shell deposits (Trant et al. 2016). Inputs of calcium increase the wood calcium levels of trees and reduce the rate of top die-back, a condition thought to be partially induced by calcium deficiency (Egan 1999, Trant et al. 2016). Furthermore, altered soil chemistry leads to increased forest diversity by shifting plant community structure on shellfish deposit sites from woody to herbaceous vegetation, resulting in more vegetative cover and higher species richness (Cook-Patton et al 2014). Fisher et al. (2019) observed that plants species with higher nutrient requirements and cultural significance persist indefinitely within culturally modified landscapes, even after intense habitation has ceased. As such, responses within primary producers occur at the landscape-level and are evident within herb, grass and tree species (Hrdlička 1937, Meigs 1938, Cook-Patton et al. 2014).

Unlike other marine subsidies, the capacity of shellfish-derived nutrients' to elicit responses within terrestrial primary producers is less spatially constrained in some aspects,

and possibly supplies important marine nutrients to terrestrial habitats lacking other subsidy pathways. For example, throughout the northeast Pacific, shellfish are deposited on many small, isolated islands with high perimeter to area ratios (e.g. peninsulas, rugged coastlines) that do not support salmon or herring spawning (Fig. 4a). Increased perimeter-to-area ratios allow for greater influx of marine nutrients by increasing vector access to marine resources, and decreasing the relative distance required for subsidies to permeate into and influence more of the terrestrial environment (Polis and Hurd 1996, Polis et al. 1997). As such, responses within terrestrial primary productivity will be the most pronounced in areas with abundant shellfish populations and low-productivity terrestrial ecosystems where species are dependent on marine resources; both of which will be highly influenced by the structural characteristics of the coastal environment.

Higher trophic level responses

Primary, secondary, tertiary and quaternary consumer responses to shellfish-derived nutrients have not been observed, potentially due to the lack of emphasis on shellfish as a spatial subsidy. As many species that consume shellfish directly or benefit from an increased abundance of species that do, also capitalize on other, better-documented marine subsidies (e.g. salmon and herring, Erlandson and Moss 2001, Gende et al. 2002, Fox et al. 2015), it is possible that these higher-level consumers respond to shellfish subsidies in similar ways. These responses would potentially include effects on population dynamics and carrying capacity, trophic interactions and physiology (Jefferies 2000). If so, responses within primary consumer populations would be influenced by shellfish-derived nutrients transferred to soil and vegetation. Responses would occur in a similar fashion to those associated with salmon subsidies, with shellfish nutrients influencing terrestrial invertebrate forest litter communities, including detritivores and certain omnivores (Hocking and Reimchen 2002), which would be detectable through increases in enriched nitrogen, but not enriched carbon (Box 1; Reimchen et al. 2003).

While we have discussed the differences between salmon and shellfish subsidies, the similarities between them support the potential cascading effects of shellfish subsidies, in addition to effects on direct consumers. If terrestrial ecosystems respond to these subsidies in similar ways, then shellfish-derived nutrients facilitate direct and indirect responses within primary, secondary, tertiary and quaternary consumer populations. For example, a plethora of secondary consumers are known to respond to influxes of marine nutrients, including dipterans and other insects (Hocking and Reimchen 2006). If these consumers respond to shellfish-derived nutrients, then shellfish remains will be colonized, supporting an increased abundance of dipteran larvae, which in turn will further disperse nutrients into terrestrial ecosystems. Christie and Reimchen (2008) demonstrated a pathway by which shellfish-derived nutrients may influence primary, secondary

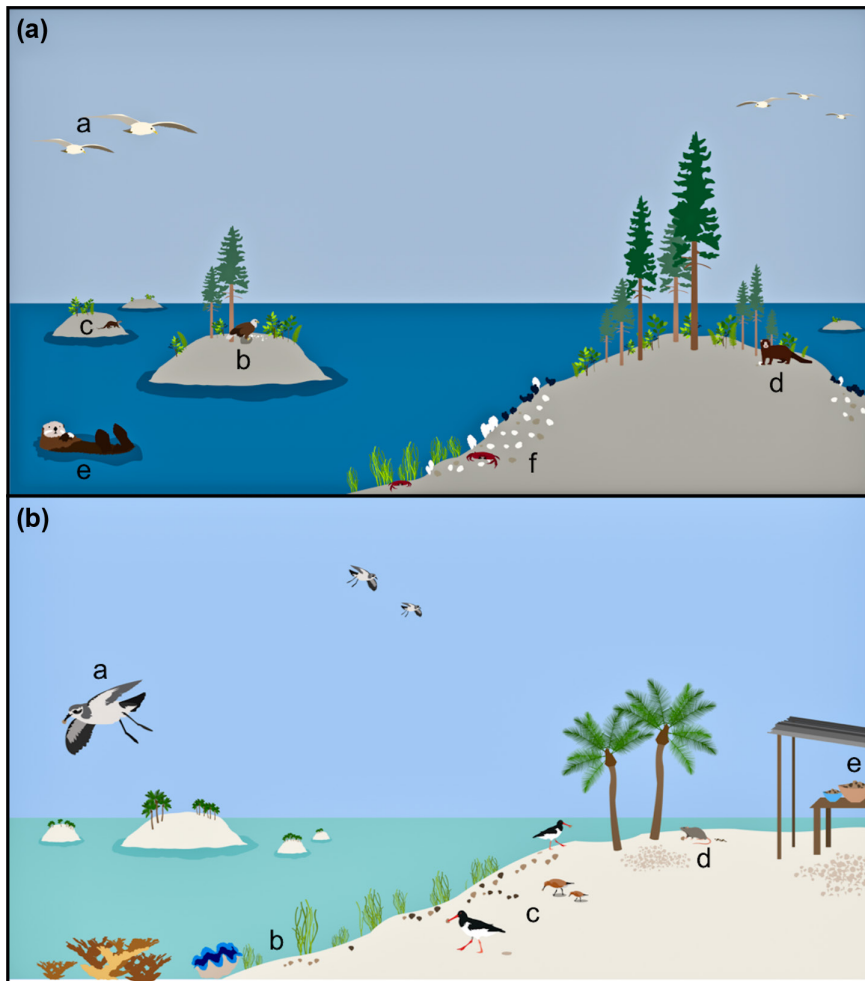


Figure 4. Vectors that transport shellfish-derived nutrients into temperate and tropical island ecosystems. (a) Temperate islands: (a–b) gulls *Larus* spp. and bald eagles *Haliaeetus leucocephalus* forage around temperate islands, consuming shellfish and discarding nutrients onto adjacent islands. (c–d) River otters *Lontra canadensis* and mink *Neovison vison* forage inter- and sub-tidally around temperate islands, returning to terrestrial areas to consume and excrete prey. (e) Sea otters *Enhydra lutris*, discard nutrients adjacent to temperate islands, frequent haul-out sites and contribute feces to temperate islands. (f) Red rock crabs *Cancer productus*, oysters (Ostreidae), mussels *Mytilus* spp., Venus clams (Veneridae) and other shellfish derived nutrients occur in high abundance surrounding temperate islands, especially relative to other potential subsidies (e.g. Pacific salmon) with pathways into terrestrial island ecosystems (e.g. lack of salmon-bearing streams). (b) Tropical islands: (a) white-faced storm petrels *Pelagodroma marina* and other seabirds commonly consume shellfish and transport nutrients via guano. (b) Giant clams *Tridacna* spp. are a major protein source in tropical locations. (c) Oystercatchers *Haematopus ostralegus*, red knots *Calidris canutus* and other intertidal shorebirds consume vast numbers of bivalves, especially west-African bloody cockle *Senilia senilis*. (d) The Norwegian rat *Rattus norvegicus* is becoming an increasingly prevalent shellfish vector as it is invasive in many ecosystems globally. (e) Evidence of shellfish collection and consumption by humans, including midden formation in areas of frequent shellfish deposition, such as beneath trees or around gathering locations.

and tertiary consumers when investigating the role of salmon in supporting higher plant productivity and invertebrate abundances, which in turn facilitates increases in songbird abundance (Fig. 3b).

Given the positive relationships between the habitat heterogeneity provided by primary producers and animal species diversity (Tews et al. 2004), impacts of shellfish-nutrients on terrestrial ecosystems would not be limited to the flow of nutrients. The previously mentioned responses in terrestrial vegetation community structure, diversity and growth would impact invertebrate, avian and even mammal ecology, based

on alterations to the physical environment, potentially providing increased habitat heterogeneity and associated niche spaces (Tews et al. 2004, Collins and Baxter 2014).

Further inquiry is needed to quantify the extent to which shellfish act as a marine subsidy, and how terrestrial responses set in motion by the input of marine derived nutrients may cascade through ecosystems. However, there is sufficient evidence to suggest that shellfish-derived marine nutrients are an integral part of coastal terrestrial ecosystems. Further investigation into the ecological role of shellfish subsidies should seek to discover the specific nutrient inputs from shellfish

in comparison to other marine-derived nutrients (e.g. macroalgae or salmon), and pinpoint the mechanisms by which shellfish-derived nutrients permeate terrestrial ecosystems (directly or indirectly). Experimental designs focused on fertilization comparisons and eDNA traces may shed light on these specific interactions, with the primary objective being to contribute a piece of the puzzle that is the holistic understanding of the diverse pathways in which marine resources influence the terrestrial environment.

Shellfish subsidies globally

The global distribution of shellfish suggests that these findings are pertinent to many other geographical regions along the marine–terrestrial interface. Ecologically, the majority of the vectors transporting shellfish into coastal ecosystems throughout the northeast Pacific have analogous counterparts globally that potentially perform similar functional roles within their respective ecosystems. Globally, arctic foxes *Vulpes lagopus*, coyotes *Canis latrans*, domestic dogs *Canis familiaris* and domestic pigs *Sus scrofa domesticus* cumulatively prey on numerous species of bivalves and crustaceans throughout North America, Greenland, South America and Eurasia, respectively (Murie 1959, West 1987, Carlton and Hodder 2003). Furthermore, many of the coastal mammals evaluated within the northeast Pacific, including river otter, mink, brown bears and raccoons, occupy substantial ranges worldwide, and would perform similar functional roles if in close proximity to a marine–terrestrial interface. At minimum, over 30 bivalve species are prey for over a dozen mammals worldwide (Carlton and Hodder 2003). A similar phenomenon is true, potentially more so given their diversity, distribution and reliance on marine resources, for coastal birds globally. Throughout the Asia-Pacific, Pacific gulls and other seabirds create 2 m wide middens containing shell fragments that are commonly mistaken for ancient deposits by coastal human populations (Jones and Allen 1978, Szabó and Amesbury 2011). These middens represent the transport of shellfish-derived nutrients into terrestrial ecosystems globally that spans millennia.

Islands

To illustrate the influence of shellfish subsidies globally, it is essential to contemplate additional environments that span ecological landscapes. Islands exhibit considerable variability in geographical structure, and with an innumerable abundance globally, they represent an extensive portion of the marine–terrestrial interface. The perimeter to area ratio of islands determines the extent that nutrients can be deposited by physical agents (Polis and Hurd 1996), with small islands most affected by ocean-borne disturbances (Neufeld et al. 2017). This suggests that as size decreases, islands become more oligotrophic and reliance on marine inputs is more extensive and instrumental compared with

large islands. Marine inputs subsidizing islands, including seabird guano and seaweeds, are known to increase nitrogen and phosphorus availability, enhance plant productivity and restructure food–web interactions (Polis and Hurd 1996, Anderson and Polis 1999, Sánchez-Piñero and Polis 2000, Piovia-Scott et al. 2011). Recently, seabird guano assimilating back into fringing marine communities and promoting the growth of ecologically essential species was illuminated (Savage 2019), highlighting the continuum that exists between marine and terrestrial nutrients in tropical marine ecosystems. Akin to the northeast Pacific, the role of shellfish, specifically molluscs, as a marine subsidy on tropical islands has not been formally described, despite extensive interactions between island species adjacent to shellfish communities, and the potential for nutrient transfer into island ecosystems (Spear et al. 2007, Szabó and Amesbury 2011, Salem et al. 2014, Thomas 2014, Fig. 4b).

An evaluation of the 30 most common seabirds in the eastern tropical Pacific Ocean determined that on average consumption of non-cephalopod invertebrates, including mollusks and crustaceans, accounted for 16% by abundance and 0.3% by mass of the average seabird diet. Although a relatively nominal percentage by mass, the population of seabirds considered consisted of between 28.5 and 35 million individuals (Spear et al. 2007), as such, even small percentages of individual diets represents a substantial amount of potential for shellfish-derived nutrients to be deposited into seabird colonies as guano. Furthermore, Spear et al. (2007) observed species of solitary feeders, particularly petrels and terns, that consumed above average amounts of epipelagic non-cephalopod invertebrates, specifically, pelagic gooseneck barnacles (*Lepas* sp.), portunid crab, crab megalops and pelagic sea snails (*Janthina* sp.). For example, members of *Stercorariidae* and *Laridae*, including the sooty tern *Onychoprion fuscata*, gray-backed tern *Onychoprion lunatus*, white tern *Gygis alba* and parasitic jaeger *Stercorarius parasiticus* consume 39.2% invertebrates by abundance and 8.4% by mass. Seasonal shorebird predation on bivalve communities is also predominant throughout tropical intertidal systems. Salem et al. (2014) evaluated predation pressure of Banc d'Arguin, Mauritania's, most dominant molluscivore, the red knot *Calidris canutus* and the less abundant oystercatcher *Haematopus ostralegus* on benthic invertebrates. Three-quarters of biomass consumed by the 300 000 seasonal shorebird population was attributed to west-African bloody cockle *Senilia senilis*. Depending on the shorebird species considered, these shellfish-derived nutrients may enter tropical terrestrial ecosystems through a variety of mechanisms, most notably through guano and discarded shell fragments (Fig. 4b).

More recently, with the global spread of invasive rats, evidence is mounting that the Norway rat *Rattus norvegicus* is influencing marine–terrestrial interactions on islands in a similar way to other invasive species (Harper and Bunbury 2015). Culminating in the global decline of a number of bird species, Norway rats are effective predators of marine molluscs, crustaceans, birds and plants (Atkinson 1985, Moors

1985, Towns and Daugherty 1994). Similar to coastal mesopredators within the northeast Pacific, the Norway rat represents a considerable vector for shellfish-derived nutrients entering terrestrial ecosystems (Fig. 4b).

Parallel to coastal human populations throughout the northeast Pacific, the importance of molluscs as a dependable source of food across the tropical islands throughout the Pacific cannot be overemphasized (Szabó and Amesbury 2011, Thomas 2014). An extensive history attests to the role of molluscs as a food resource for non-sapiens hominids and early modern humans throughout the Asia-Pacific (Choi and Driwantoro 2007, Stringer et al. 2008). Evident throughout the Pleistocene and Holocene, modern humans' relationship with shellfish for sustenance and tool use is clearly visible in shell middens deposited throughout the Asia-Pacific region. Many of which coincide with the first appearance of modern humans in the region, and draw a strong link between pressure on shellfish populations and human population growth (Klein et al. 2004, Szabó and Amesbury 2011). Early utilization of shellfish largely targeted freshwater species (O'Connor et al. 2002), with mid to late Holocene middens throughout the region reflecting an increased focus on marine mollusc species, including *Meretrix meretrix*, *Anadara antiquata* and *Strombus gibberulus gibbosus*, depending on the ecological conditions of the site (Szabó and Amesbury 2011). The importance of shellfish within tropical ecosystems has persisted since the first appearance of modern humans into contemporary island cultures, especially on atolls and low coral islands that lack fertile soils and perennial surface freshwater (Thomas 2014). With over 300 atolls and low coral islands in the Pacific Islands region, including the Tuamotu, Marshall Islands, Tuvalu and Kiribati, these regions exemplify the marine-terrestrial interface, and importance of subsisting on and managing marine subsidies (Thomas 2014, Watson et al. 2016). Currently on Kiribati, combined shellfish catches can exceed 40% by weight of landed marine resources, with as high as 10% of households depending on shellfish, largely *Anadara uropigimelana*, *Tridacna gigas* and *Tridacna maxima*, as their main protein source (Thomas 2014). Much like consumption of shellfish nutrients throughout the Pacific northeast, this consumption results in the deposition of large middens, potentially spanning meters and persisting indefinitely (Fig. 4b).

Global human populations

The relationship between coastal human populations and shellfish-derived nutrients is not limited to the northeast Pacific. This relationship may be especially evident within the northeast Pacific due to the rich cultural history of the region, a wealth of Traditional Ecological Knowledge, and substantial research efforts (Deur et al. 2015, Lepofsky et al. 2015, Trant et al. 2016, Fisher et al. 2019); however, systematic utilization of shellfish by coastal populations is a global occurrence. For example, two shell middens, Sea Harvest and Hoedjies Punt in Saldanha Bay, South Africa, suggest coastal populations have been depositing shellfish-derived nutrients into terrestrial ecosystems for a minimum of 60 000–70

000 yr before present (Volman 1978). In both instances, the biological material within these middens is composed predominantly of molluscs. Furthermore, 100 km north along the western Cape coast of South Africa, shellfish gathering from mid to low-intertidal zones was consistent throughout the late Holocene, with collections spanning further into the upper subtidal within the last 600 yr (Jerardino 1997). The excavation of the Pancho's Kitchen Midden, in Elands Bay, South Africa, illustrates shellfish harvesting in the region beginning at minimum 3500 yr before present and resulted in a stratified shellfish midden comprised of between 75 and 99% percent black mussels *Choromytilus meridionalis* across several defined layers (Jerardino 1997). Similarly, evidence of the relationship between coastal human populations and shellfish-derived nutrients has been observed throughout the Pacific Line Islands (Thomas, 2014), the Asia-Pacific (Szabó and Amesbury 2011), Australia (Bird et al. 2002), and throughout north-west Europe (Schulting et al. 2004).

Despite being less evident within contemporary culture, the removal of molluscs and other shellfish from marine ecosystems by coastal human populations is a global phenomenon, elevated due to expansion of aquaculture (FAO 2016). Currently, 18.8 million metric tons of non-cephalopod molluscs are landed annually by wild and aquaculture fisheries (FAO 2016), which comprise 11% of all global seafood production. Although the role this transfer of nutrients plays within terrestrial ecosystems remains unknown, if even a fraction of these nutrients enters terrestrial ecosystems, the potential for ecological responses is evident. As annual seafood consumption is set to increase by 1.5 kg per person in the coming decade (Delgado et al. 2003, FAO 2016), and especially as shellfish farming is incorporated in marine planning initiatives and developed with local ecological context (Holden et al. 2019), any effect on terrestrial ecosystems related to shellfish removal by industrial fisheries will only increase.

Conclusions

The current focus of spatial subsidies has been aimed at large nutrient-rich pulses, such as spawning Pacific salmon, that result in dramatic ecosystem responses. However, studies are increasingly showing that there are multiple avenues of marine subsidy acting to influence coastal terrestrial ecosystems (Ben-David et al. 1998, Spiller et al. 2010, Fox et al. 2015). Shellfish as a marine subsidy has received relatively less attention than many other sources of marine nutrients. Here we have summarized the known information regarding vectors of shellfish transfer to land, as well as documented and hypothesized effects to the adjacent terrestrial ecosystems. Given that shellfish are released from many temporal and spatial constraints imposed upon other marine subsidies, we suggest that they are an important, but under-represented source of marine nutrients. While recent archaeological work is beginning to shed light on the importance of shellfish on land (Trant et al. 2016), there is still much to be done to understand the role of shellfish subsidies across larger

spatial and temporal scales, and the impacts on multiple trophic levels.

Wild shellfish populations, much like salmon and seabird colonies, have suffered drastic reductions due to harvesting, habitat degradation and climate change. As an integral part of coastal ecosystems globally, further declines in shellfish populations will undoubtedly have far-reaching consequences. As such, there is a need to understand the extent that shellfish-derived nutrients contribute to terrestrial ecosystems, if the diverse coastal ecosystems shellfish have supported for millennia are to be maintained.

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